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THE GROWTH OF BIRDWINGS

K. Meunier

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THE GROWTH OF BIRDWINGS

With 8 Figures and 9 Tables

K. Meunier¹

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I. Growth Allometry and Order Allometry

/444*

1. Intraspecific and Interspecific Proportion Shifts in Adult Birds

In my earlier experiments (Meunier, 1951) I stated that a comparison of adult birds shows birdwings to be allometrically negative in relation to the body. This holds true within a species for probably all species of birds. It is also true among species for the German gulls, Larus ridibundus, canus, fiscus, argentatus, and marinus, which are of the same or very similar flying types. This discovery was statistically proven and has since been further researched and confirmed by Dinnendahl and Kramer (1957) in a very detailed study on gulls. These two authors extended this discovery with the addition of the important fact that probably only the feathers are involved in allometry. The length of the wingbones or manner in which they influence the wing surface is isometric between species.

I studied allometry in two different ways:

- a) By comparing the wing length with the spinal column. Wing length is designated in ornithological taxonomy as the area of the closed wing from the wrist to the wing tip. It is primarily an expression of the length of the longest primary.
- b) By comparing the wing surface and weight (S and W respectively). /445
Since these values change, it is necessary for allometric studies

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* Numbers in the margin indicate pagination in the foreign text.

to reduce them to linear values. The allometric equation thus appears as

$$\sqrt{S} = b\sqrt[3]{G}^{a-1}$$

The wing surface does, of course, change with the degree of spread, and it is therefore very difficult to make intraspecific comparisons with sufficient precision. In my earlier experiments I drew my wings in one of the natural positions of normal flight. I now stretch out each wing, regardless of its continually changing positions during flight, to the point where the outer edge forms a more or less straight line in so far as this is possible (Figure 8). Care must be taken that the angle formed by the last primary and the front edge of the wing is always the same. These methodic details are important since there are only minimal differences in intraspecific comparisons. Dinnendahl and Kramer additionally used another method in which they took a set of certain basic dimensions of the wing as representative of the surface and compared the resulting diagrams. They used this method primarily in interspecific studies and the similar results found are of great value since the method of direct diagrams is subject to automatic control. For determining intraspecific allometries, however, the diagram method is an unsure one. The relative primary lengths sometimes vary greatly from individual to individual, and it seems better to me to avoid the loss of these differences that results with the diagram method.

If we compare an intraspecific series of weights and wings using the allometric equation as mentioned above, we always obtain exponent values considerably under 1. I have listed the constants for a series of species in Table 1, column A. This is the first time these figures have been released, but they are taken from material on which my earlier publication was based but which was evaluated in a different manner there. The allometric exponents given there are misleading for a reason which needs to be more closely examined here owing to its general

¹The exponent is often designated by a , but since this also designates the angle of inclination, the choice is unfortunate. The formerly

significance. A series of individual birds is always in a different dietary condition. This is also the case when all individuals are collected at the same time of year and in the same circumstances. The different dietary conditions cause fat individuals to be treated as larger than they really are and their wings to be compared to too great a body weight. Conversely, thin individuals are given lower values than

/446

Table 1

Intraspecific allometric constants (exponent a) of the wing

A. $\sqrt{\text{wings}}$ as a function of $\sqrt[3]{\text{empirical weight}}$

B. $\sqrt{\text{wings}}$ as a function of $\sqrt[3]{\text{normal weight}}$

C. wing lengths (primaries) as a function of the AS length (spinal column)

Species	Number	A	B	C
Common starling Sturnus v. vulgaris	54	0.295	0.516	0.315
Common guillemot Uria aalge albionis	44	--	0.421	--
Velvet scoter Melitta f. fusca	35	0.327	0.824	0.726
Black-headed gull Larus r. ridibundus	25	0.484	1.310	0.614
Mew gull Larus c. canus	52	0.501	0.735	0.575
Herring gull Larus fuscus intermedius	52	0.629	0.808	0.608
Silvery gull Larus argentatus argenteus	75	0.499	0.895	0.596
Great black-backed gull, adult Larus m. marinus	19	0.328	0.500	0.386
Great black-backed gull, juv. Larus m. marinus	53	--	0.576	0.584

common symbol x is also a poor one, since it also designates an exponential function when used with exponents.

corresponds to their wings. This would also result in negative /446 allometry when the values are actually isometric. This error cannot be overcome by increasing the number of individuals. I overcome it by adjusting the weights according to the AS length.

Care must be taken that the cube root of the weight does not change proportionally to the spinal column but allometrically. Therefore, the calculation of normal weight cannot be determined simply by calculating the average of individual values obtained through $\frac{\sqrt[3]{G}}{AG}$. Instead, it must be determined for each AS length. (For further material, cf. /447 Meunier, 1951, p. 416.)¹ I designate the weight values obtained in this way as being normal weights. They correspond to the medium dietary condition of the series for each spinal column length.

As was expected, the exponent values increased when this correction was used. They remain, however, entirely negative with the exception of the black-headed gull series (Table 1, column B). The value indicated for the black-headed gull is undoubtedly not indicative of reality but determined by statistical chance. The series exhibited particularly uneven dietary conditions. The allometric constants in column C relative to dependence of wing length on the spinal column indicate negative allometry even for the black-headed gull.

The effect of condition must be considered in all allometric studies in which body weight is used as a reference value but in which the size of the organ under consideration is not affected by dietary condition. Eliminating this effect is not always so easy, and it can be a source of errors with birds. It is certain, however, that the results obtained in this manner better reflect true allometric relationships than those of column A obtained without weight correction.

¹ Dinnendahl and Kramer suggested a similar procedure involving the replacement of the cube root of the weight by the sum of a number of skeletal lengths. This method may be more precise and is of particular use for interspecific comparisons. It is too complicated for studying large intraspecific series, whereas the AS length is quick and easy to determine from a bird's hide.

2. Ontogenetic Proportion Development

The presence of negative wing allometry within a species was surprising since it had already been stated that it would contradict ontogenetic allometry. A bird's primary feathers begin to grow only after the body has reached a considerable size. They are thus behind in growth and catch up with the body only after a period of time. This implies that their growth, when measured against the entire body or against some part that is representative of body size, must be allometrically positive. This can be confirmed through direct measurement of growing birds. I take as an example my curve of the primary lengths of growing herring gulls (Figure 1), which is based on data taken from Heinroth (1931).

This curve is a characteristic picture of positive allometry with the exception of the fact that the 0 values of x and y do not come together. Therefore, this curve cannot be computed through the usual allometric equation, $y = bx^3$ but demands the introduction of a third constant p, which represents the pre-existing body size. It must be introduced in the equation as follows:

$$y = b(x-p)^3.$$

The value of p can be empirically determined immediately. It is 4 in the figure, which is a linear expression of the fact that primary /448 growth begins at a weight of 64 grams ($\sqrt[3]{64} = 4$) for the herring gulls studied.

The significance of an additive constant for the allometric equation was to my knowledge first recognized by Robb (1929). He introduced it in the form $y = bx^a + c$, and was able to improve the approximation of empirical data through its use. The general significance of an additive constant lies in the fact that only through its use can the mathematical possibilities of the function be exhausted.

Allometric research originally supposed that an allometric comparison of adult animals of the same species but different sizes

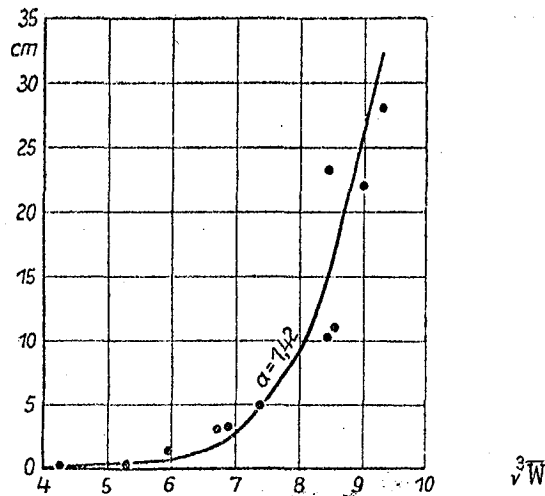


Figure 1. Measurement of the longest primaries as a function of the cube root of the weights of two adolescent herring gulls (*Larus fuscus*). Calculated according to data taken from Heinroth. Numerical graph.

sizes would result in identical allometry, as is the case with growth. An immediate explanation is offered by the fact that larger individuals grow longer than smaller ones and thus undergo a longer allometric process. Frequent failures to keep separate the growth studies performed on adult individuals of different sizes can often be overlooked, but it is not permissible in the case of the birdwing. Identical allometry cannot be assumed in this case and must be calculated for each individual.

3. The Order Principle

/449

In the search for an explanation to proven allometric inversions, the theory was first advanced that feathers do not have positive allometric values during the entire period of growth until the very end when they grow slower than the body. Of course, the allometry of adult individuals can agree only with the allometry of the period of ontogenesis. There is, however, no indication of this sort of turning point. The curve of feather growth as a function of body growth is not S-shaped in all cases with which I am acquainted but becomes vertical towards the end instead, since the young bird acquires its adult

weight sooner than it acquires its final wing length.¹

The diagram in Figure 2 shows how the allometric inversion actually takes place. The supposition that statistic allometries are the result

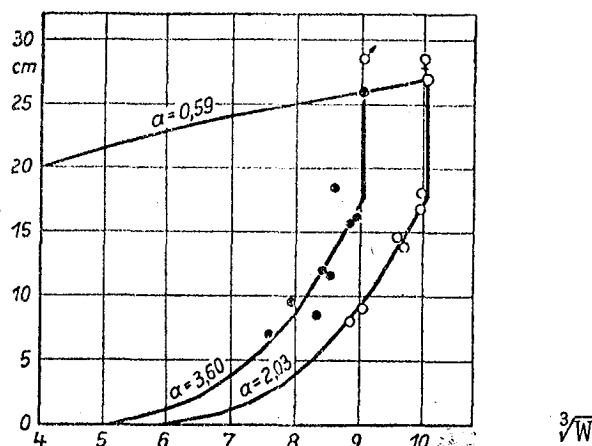


Figure 2. Diagram of the wing allometry of the hawk (Accipiter gentilis). Wing length: cube root of the weight. Filled circles 2 males, empty circles 2 females. Allometrically positive growth, placement of curves determined by final size. Adult individuals allometrically negative. Numerical graph.

of growth allometries is based on the assumption that large individuals follow the same growth patterns as small individuals. This is obviously not the case with the growth of primaries. I selected the hawk for this study (Accipiter gentilis) because the size difference between the sexes is so large that there is no danger of confusing the measurements, and I raised two males and two females simultaneously. The diagram is of particular interest since the measurements of both growing /450 stages and grown individuals taken from the same birds. The large individuals (females)² do not follow the same growth patterns as the small ones but establish their own curve from the very beginning. Thus, right from the start the growth curves are determined in such a way that the curves of the larger adults studies lie under those of

¹ The ratio for adolescent birds still in the nest but capable of flight is more complicated; I do not know them in detail.

² Translator's note: Mr. Meunier uses the biological symbols for male and female in his text. It is possible that he confused them at some points.

of the smaller individuals, i.e., for a given individual the larger individuals have shorter feathers. This can be readily understood from the fact that the same size level indicates an earlier stage of development for the larger bird. As I demonstrated in 1951 in my evaluation of a study on common crows done by Heinroth (1924-26), the growth process can take place in such a way that the smaller individuals have shorter feathers than the larger birds in the beginning and acquire longer feathers for a given weight later on, thus causing the curves to intersect. This curve juxtaposition is ideally shown in the case of the hawk because of the very great difference in size. In the case of birds with less size discrepancy the curves can become confused. The important factor, however, is the relative positions of the curves at the adult size of the individuals, whether this is established in the beginning or during growth. This juxtaposition emphasizes the negative wing allometry of adult birds rather than growth allometry as such. However, when statistical and ontogenetical allometries are the same, it is unimportant which birds become the large ones and which the small.

This obviously implies two completely different and independent forms of allometry that cannot be limited to birdwings alone. The information provided by them is probably distorted many times through the fact that ontogenetic stages and adult animals of different sizes are mixed in studies where the limited number of individuals used and the magnitude of distribution hinder the extent to which discrepancies can be recognized, particularly when no complete allometric inversion takes place but only a small shift.

I do not find the necessary differentiation for these cases in the literature nor in the definitions of Huxley, Heedham, and Lerner (1941). They distinguish between:

heterauxesis = the allometry of ontogenesis

allomorphosis = the allometric variations of breeds, varieties, species, and genera

It is impossible to find a meaningful organization for the problems arising from birdwings using this distinction. The allometry of /451

the adult stages does derive from ontogenesis, but it does not arise as thought from the allometry of growth itself. I feel it is necessary to separate these terms completely and to divide heterauxesis as follows:

growth allometry (allotrophy):

The allometric process of growth and its application to individuals according to basic principle.

order allometry (allotaxis):

The allometric juxtaposition of comparable adults, i.e., adults that do not belong to separate groups.

This theory agrees fundamentally with that of Dinnendahl and Kramer (op. cit., p. 327) in which the relative ratios of growth serve to fulfill the proportion plan, which is understood as being the hereditary plan causing specific proportions to achieve specific adult sizes. I do not, however, agree with the simultaneously advanced idea that allometric inversion is the obvious consequence of this and that the growth of birdwings is "preparation growth" just as brain growth, as opposed to the "function-determined growth" of crocodiles and ametabolic anthropodes whose proportions change in direct relationship to their respective functions. To consider wing growth as being parallel to prenatal brain growth is correct in so far as both growths prepare for the functions of future stages, but there is no system of allometric relations. We are referring here to the relationship of the growth of an organ to the growth of the rest of the body, and in this birdwing growth and brain growth are opposed. Prenatal brain growth is faster than that of the rest of the body, which explains why it is allometrically negative after birth. Wing growth, however, lags behind the growth of the overall body initially and leads necessarily to positive allometry later on. Fast or lagging growth can explain only individual allometries but not the inversion that occurs between the two forms of allometry, which is also not a turning point in the ontogenetic curve.

It must be quite clear that the use of the allometric equation in problems beyond those of strict ontogenesis, such as its application to order allometries, does not have the same explanatory value as with growth allometries. It results in both a description and a rational

explanation of the growth curve in the case of the latter (cf. /452 Bertalanffy, 1951, pp. 272-75). Its use on purely relative allometries is merely descriptive. Allometry here means nothing more than a regular shift of proportions in relation to body size but says nothing about the causes of this shift. However, the allometric equation is indispensable even for pure description since it enables definition of a given curve and thus makes possible comparison of different objects with few constants.

II. Body Size and Flight Power

1. The Law of Increasing Wing Loading and Wing Allometry

If we suppose a bird to have increased its size while retaining its linear proportions, its weight (W) increases to the cube of the linear increase, but the wing surface (S) increases only to the square of the linear increase. The wing loading $\frac{W}{S}$ increases in proportion to linear size increase. Thus, a bird whose size has been doubled increases its weight by a factor of 8, its wings by a factor of 4, and its wing loading by a factor of 2. This law of increasing wing loading is a special case of the surface law and has no direct bearing on allometric ratios. This has always been regarded as the reason for a size limitation for birds capable of flight since it demonstrates with unmistakable clarity that wing loading eventually has to reach a level during steadily increasing body size where flight becomes impossible. This includes the fact that any possible changes in body type concomitant with the increase in size, which counteract the increase in loading (acquisition of a relatively large wing, change in the wing form, relative strengthening of the flight muscles) do raise the critical limit but cannot remove it since it cannot be increased indefinitely.

In my work already mentioned above I presumed this theory to be universally accepted and extended it using known allometric ratios to show that when the negative allometry of a species is retained during an evolutionary size increase of that species, the upper size limit for flight capability is necessarily reached at a much smaller body size than when a proportional size increase occurs. This conclusion

is, of course, only conditional. Whether or not phylogenetic increases have actually taken place without changing intraspecific allometry is still a moot point and must be studied in each individual case. My conclusion cannot be attacked as such. To do so, as have Dinnendahl /453 and Kramer (op. cit., both orally and in writing by Mr. Kramer) is to call into question the fundamental theory of size limitation through the surface law, on which my conclusion is based. To my great surprise, the authors mention only my name in this regard and never once state that this is a generally accepted idea. Yet Stresemann wrote as follows (1927/34, p. 597): "...with increasing body size the birdwing loading increases as does the speed necessary for soaring whereas muscular capabilities decrease. Thus the size development of flying birds is subject to an upper limit. Going beyond this limit necessarily results in a loss of flying capability..." More recently, Savile (1957, p. 216) examined the question of increased wing loading. He writes: "Thus, in birds that are otherwise similar, one with a 12 inch span, will have twice the wing loading (weight per unit area) of one with a six inch span. We see at once, why the upper weight limit is so much smaller for flying than for flightless birds. It is also clear that the lift problem is much more acute for large birds than for small ones." The work of Portmann (1957, pp. 91-93) is also quite clear. I thus fail to see why I alone am held responsible for this "misinterpretation."

Stresemann's work in particular provides numerous data that back up the theory. The upper size limit is about 15 kilograms for flying birds (Pelecanus, Cygnus) whereas the ratites can achieve weights up to 90 kilograms (Struthio), and flightless fossile forms (Aepyornithes and many others) weighed considerably more. The largest members of groups of flying birds are often flightless as well, such as the fossile goose Cnemiornis calcitrans, the steamer duck Tachyeres cinereus, and the great auk Pinguinus impennis. It is of no consequence to the aerodynamic side of the question whether in a specific case the great size brought about the loss of flight or whether the loss of flight capability made the great size possible.

Thus Dinnendahl and Kramer's argument against what appear to be clear facts is quite serious and demands extensive examination. They base their argument on the fact that for aerodynamic reasons the wing loading of a larger bird must be greater than that of a smaller bird. This has been affirmed in ornithology many times before (Lorenz, 1933, von Holst, 1943). Dinnendahl and Kramer maintain that the wing loading increase accompanying a proportional size increase is insufficient to meet aerodynamic requirements and is thus adaptively strengthened by negative wing allometry. They base themselves on the fact that since /454 wing allometry is an order allometry and thus not necessarily produced by allometric growth, it is probably determined by functional adaptation.

In order to test this theory, we need to examine the aerodynamic basis for the necessity that wing loading increase when body size increases. The symbols used in the following explanations are listed and explained in Table 2.

Table 2

Explanation of aerodynamic symbols

ϵ = atmospheric density near the Earth's surface 0.125

η = atmospheric resistance

t = wing chord (width), calculated for birds as the average quotient of the surface and length of the outstretched wing

c_a = lift coefficient

c_w = resistance coefficient

Calculated from atmospheric pressure equations:

$$R = c_w \cdot \frac{1}{2} \epsilon v^2 \cdot S$$

S = wing surface

W = weight

$$L = c_a \cdot \frac{1}{2} \epsilon v^2 \cdot S$$

R = resistance

L = lift (identical with W for a flying body)

$$v = \text{angle speed} = \sqrt{\frac{W}{S} \cdot \frac{2}{\epsilon} \cdot \frac{1}{\sqrt{c_a^2 + c_w^3}}}$$

$$\text{in the case of flat gliding} = \sqrt{\frac{16 \cdot G}{1} \cdot \frac{1}{c_a}}$$

Table 2, cont.

$$v_y = \text{rate of descent} = \sqrt{\frac{G}{F} \cdot \frac{2}{\epsilon} \frac{c_w^2}{c_a^2}}$$

v_x = horizontal speed, can be replaced by v for flat gliding

ϵ = glide ratio, indicates the horizontal glide for a fall height of 1 meter. Improves by a factor of 2 for a linear size increase of a factor of 10 (in Table 3 from 1:10 to 1:20). It is always calculated with the best glide ratio, i.e., the best initial angle.

The formula is

$$\epsilon = \frac{c_w}{c_a} = \frac{R}{L} = \frac{v_y}{v_x}$$

The phenomenon is based on the following condition: in the case of gliders and their identically shaped models, airstreams do not travel in the same way. since the acceleration effect of the air $\epsilon v^2 t^3$ increases faster than the resistance effect $\eta v t^2$ as the aircraft size /455 increases. The ratio of the two is expressed by the Reynolds number:

$$Re = \frac{\epsilon v^2 t^3}{\eta v t^2} = \frac{\epsilon v t}{\eta}$$

The variable $\frac{\epsilon}{\eta}$ (= kinetic resistance) can be assumed to be 70 for the lower atmospheric layers resulting in the simple equation $Re = v \cdot t \cdot 70$. Since the absolute size of the aircraft as represented by the wing chord t is reduced in the Re number, it must acquire a higher value with increased size. This means that the ratio resistance to lift changes in favor of the lift in the case of large aircraft as opposed to a model. Birds fly like aircraft models as absolute small flying bodies with low Re numbers but would acquire larger Re numbers with size increase. Owing to the increase in lift over resistance, a higher wing loading is not only possible but actually promoted.

These facts and in particular their quantitative basis were more precisely determined in the basic research of Schmitz (1957, first edition 1942) on the aerodynamics of a aircraft model. Dinnendahl and Kramer base themselves primarily on the results of this author and

cite the table in which he compiled those results (Schmitz, op. cit., p. 18). I have compiled the most important information of this table, which is the change in aerodynamic data from the glider model to the actual glider. In order to understand this table and its possible biological significance, it must be realized that the biologist is not in the same position as the airplane engineer. The latter assumes that a size increase without any change in shape will retain the same proportions and not cause an automatic weight reduction. It is largely possible for him to determine weight arbitrarily in order to adapt it to aerodynamic requirements. However, an increase in bird size without a change in form automatically increases the load by a factor corresponding to the size increase. Schmitz chose his glider model wing loading to correspond to the rate of descent of the large aircraft, which means the same length of gliding time and the same climbing ability in updrafts or the same overall gliding ability. However, the aerodynamically determined wing loading of an aircraft whose size has undergone a linear increase of a factor of 10 is not 10 but only 8 times as great (Table 3). This result is a decisive one for our purposes. In comparison with the small model, the glider is not an isometric size increase in the biological sense despite "identical shapes," but is actually allometrically positive as regards the relative wing surface increase. /456 If the wing surface increase were proportional, the glider would not achieve identical flight capabilities but be overburdened. Dinnendahl and Kramer failed to take this quantitative aspect of the question into account.

Based on these facts we can attempt to depict the aerodynamic characteristics of a bird whose size has been tremendously increased. Schmitz included the silvery gull in his table. He obtained the morphological data on this bird from me in 1942 and combined it with data on speed and glide ratios whose origin I do not know. I borrowed the data on normal sized gulls in my Table 4 and used them as a basis for calculating the corresponding values for gulls of aircraft size. Schmitz discovered empirically that where a linear size increase of a factor of 10 takes place the glide ratio improves by a factor of 2 as a reflection of the increased Re number.

Table 3

Aircraft model and glider according to Schmitz 1957, p. 18

Aircraft	Wing- spread	Wing surface S	Weight W	Wing loading W S	Best glide ratio ϵ	Rate of des- cent $v_y = \epsilon v$	Glid- ing speed v	c_a
	m	m ²	kg	kg/m ²		msec	msec	
Aircraft model	1.3	0.17	0.34	2	1:10	0.8	8	0.5
Glider	13	17	270	16	1:20	0.8	16	1.0

It is assumed with gull B that the wing loading increases as it did from glider model to glider, i.e., by a factor of 8. It is further assumed that this gull has the same gliding capability or same rate of descent of 0.67 as the silvery gull A. The comparison is well founded since silvery gulls and glider models on the one hand and mamouth gulls and gliders on the other hand have the same wing spread and wing surfaces. All other data can be automatically calculated: the c_a value of the mamouth gull is thus twice as large as that of the silvery gull, as is the case with the glider to model ratio (Table 3). A gull /457 that could fly at this mamouth size¹ would have undergone allometrically positive wing increases.

Gull C is a hypothetical isometric size increase and gull D is allometrically negative based on the intraspecific wing allometry of the silvery gull. The question arose with the two of them how the c_a value should be calculated for determining speeds. This was done for B based on the rate of descent of 0.67 milliseconds. It would not be a major error to calculate c_a for B based on 1.87 milliseconds since the same order of magnitude is concerned here. We are merely trying to illustrate the principle of the effects that an extreme size increase

¹ From the standpoint of wing loading! Such an animal would, of course, be incapable of flight owing to physical properties, leverage ratios, muscle performance (cf. Buddenbrock, 1934), and the unevenness of wing surfaces.

would produce. Contrary to B, the mammoth gulls C and D are not conceived according to aerodynamic requirements but rather, according to isometry and intraspecific allometry. The increase in rate of descent of these gulls indicates that they would not have the same gliding capability as the silvery gull A. In order to evaluate their flight capabilities, the calculation of minimal performance requirements can be used. This is the capacity that an aircraft must possess in order to be able to fly horizontally, whether through updrafts or a motor. It is expressed in mkg/sec and is equal to the product of speed in milliseconds and resistance in kilograms. The minimal capacities shown in the table for C and D could not be achieved with updrafts, which is undoubtedly linked to the fact that gliders of this size and high wing loading are not constructed. Thomsen's work (1953) leads me to believe that glider types having a wingspread of 12.6 to 18.3 meters and 16 to 21 m² wing surfaces have wing loadings of 12 to 24 kilograms at full flying weight. The increase in rate of descent can be counteracted for gliding only by stronger updrafts, which are subject to an upper limit. The fact that larger gliders can require overly proportional minimal capabilities and thus be dependent on stronger updrafts is extended by Savile (op. cit., p. 219) to the specific case of the albatross: "It is probably not due to chance that this species (*Diomedea exulans*) and the almost equally large Royal Albatross (*Diomedea epomophora*) are practically confined to latitudes 30-60° S, the region of strong and almost continuous southern westerlies in which mechanical up-drafts are generally powerful. In contrast several of the smaller albatross range north through the doldrums and horse latitudes where air circulation is generally weak."

I attempted in the last columns of Table 4 to compare minimal /459 capacity with maximum possible muscle performance. It is presumed here that the flight muscles retain the same proportions of body weight during size increase. When capacity is increased in proportion to weight, muscle power is squared (on the average) and vertical lift increases by the factor of linear size increase.¹

Table 4

/458

The aerodynamic characteristics of silvery gulls increased to airplane size

Model	Wing spread	Wing sur- face S	Weight W	Wing loading W S	Best glide ratio ϵ	Rate of des- cent $v_y = v \cdot \epsilon$	Gliding speed v	c_a	Resis- tance $R=W^2$	Performance requirement $v \cdot W$	Muscle perfor- mance
	m	m ²	kg	kg/m ²		msec	msec		kg	absolute mkg/ sec	relative relative
A. Real gull	1.3	0.17	1	5.9	1:15	0.67	10.0	0.94	0.0667	0.667	1
B. Wing surface in- creased, allometri- cally positive	13.0	17.0	804	47.2	1:30	0.67	20.1	1.87	26.8	538	804
C. Wing surface in- creased, isometric	13.0	17.0	1000	59.0	1:30	0.75	22.4	1.87	33.3	746	1000
D. Wing surface in- creased, allometri- cally negative	13.0	17.0	1085	63.8	1:30	0.78	23.3	1.87	36.1	841	1085

It is clear that the muscle structure cannot keep abreast of the performance requirement. Motor aircraft with a wing spread of 10.2 to 11.1 meters, a wing surface of 13.6 to 18.8 m², and a wing loading of 62 to 76 kg/m², or a performance requirement comparable to that of the hypothetical mamouth gull, have, according to Thomsen, a motor capacity of 145 to 260 horse power or approximately 1100 to 1950 mkg/sec. They have a top speed of 50 to 75 milliseconds. These rates are fully comparable to those demanded by the table and the result of our calculation is that the mamouth gulls C and D could not fly because they would be too heavily burdened. The fact that this size aircraft is available to us today with far greater wing loading is made possible by the greater speeds achieved by improved motor performance, but this possibility is closed to the living organism. This result refutes the argument against size limitation on the basis of the law of increased wing loading. Savile has addressed this question (op. cit., p. 219) with particular reference to soaring birds: "Clearly there must be an upper size limit for soaring birds, because wing area cannot be indefinitely extended to keep pace with weight, which we recall increases as the cube of the linear dimension. The figures given are for a large specimen of the Wandering Albatross (refers to the data in my Table 8, M.). The high wing loading suggests that this species has just about reached the practical limit of size..."

2. Small and Extreme Size Differences

We find ourselves thus confronted by the following antimony:

- a) in the case of minimal size differences within species and in the somewhat wider range of the small to large species of gulls, the increase in wing surfaces is underproportional (allometrically negative)
- b) in the major jump from the aircraft model to the airplane and, /461

¹ Size-dependent energy expenditure per unit of weight is not taken into account (cf. Buddenbrock, 1934). This in turn determines size limitation in the extent to which the allometry of heart size influences muscle performance (cf. Wagner, Festschr., Stresemann,

Table 5

/460

Aerodynamic data of gull species of different sizes with varying glide ratios and gliding speeds within each species:

Line 1: according to Dinnendahl and Kramer, 1957, Table 1

Line 2: using a rate of descent of 0.67 and retaining the gliding speed of Line 1

Line 3: using a rate of descent of 0.67 and retaining the glide ratio of Line 1

Species	Weight W kg	Wing loading $\frac{W}{S}$ kg/m ²	Best glide ratio ϵ	Rate of descent $\frac{v_y}{v} = \epsilon$ msec	Gliding speed v msec	Lift coefficient c_a	Resis- tance $R=W \cdot \epsilon$ kg	Performance requirement $v \cdot \epsilon$ absolute relative mkg/sec		Muscle perfor- mance relative
Larus ridibundus	0.23	3.07	1:13.3	0.58	7.7	0.83	0.0173	0.133	1.00	1.00
			1:11.5	0.67	7.7		0.0200	0.154	1.00	
			1:13.3	0.67	8.9		0.0173	0.154	1.00	
Larus canus	0.40	3.51	1:14.2	0.55	7.8	0.92	0.0282	0.220	1.65	1.74
			1:11.6	0.67	7.8		0.0375	0.269	1.74	
			1:14.2	0.67	9.5		0.0282	0.269	1.74	
Larus argentatus	1.00	5.88	1:15.0	0.67	10.0	0.94	0.0667	0.0667	5.02	4.36
			1:15.0	0.67	10.0		0.0667	0.0667	4.36	
			1:15.0	0.67	10.0		0.0667	0.0667	4.36	
Larus marinus	1.60	6.90	1:15.8	0.66	10.5	1.00	0.1012	1.062	7.99	6.90
			1:15.7	0.67	10.5		0.1019	1.1062	6.90	
			1:15.8	0.67	10.5		0.1012	1.1062	6.90	

clearly, from a model-sized bird to an airplane-sized bird of the same build, the increase in wing surface must be overproportional in order to maintain the same flight capability (allometrically positive).

In view of this contradiction the tendency is to consider negative allometry as an imperative process denying functional requirements. We have seen, however, that this cannot be assumed. Dinnendahl and Kramer published (op. cit., p. 299) a compilation in their Table 1 of probable aerodynamic data concerning the four species of gulls they studied. These data are of great interest since they undoubtedly contain the secret sought. Dinnendahl and Kramer have two points of departure for their calculations: the data of Schmitz on silvery gulls and his realization that the glide ratio of an aircraft doubles when the size is increased by a factor of 10. This enables them to calculate the proportional changes in glide ratios based on size change. It is not clear from their work how they calculated the speed of the other species. This can be calculated using the formulas for the glide ratio and speed of descent (cf. Table 2 above) only when the lift value c_a is known, which in turn can be calculated only when the glide ratio is known. I have taken the results of Dinnendahl and Kramer's table verbatim in my own Table 5 (Line 1 for each species of gull). In addition I calculated the c_a values using the speeds indicated by Dinnendahl and Kramer. The main result of computer comparison is a decrease in the glide ratio for smaller species. Dinnendahl and Kramer combine their computer aerodynamic study with field observation to demonstrate quite justifiably that large species of gulls soar better, not worse, than the smaller ones. They appear to assume that the improved glide ratio is indicative of their observation and proves the adaptive nature of negative allometry. This is a mistake, since, as we have seen, glide capability in an up-draft is not determined by the glide ratio but by the speed of

Heidelberg, 1949).

descent.¹ The table shows the speed of descent as being bigger for large gulls (0.67 milliseconds) than for small gulls (0.55 to 0.58 milliseconds). If this were to be true, these two authors would have proof of the very theory they oppose! Their work on the wind susceptibility of minimally burdened soaring birds (op. cit., p. 303) is quite relevant and can well be applied to the distribution ecology of the black-headed gull on the one hand and the great black-backed gull on the other hand (exclusively inland and sea birds, respectively). This does not, however, solve the question of performance requirements. Furthermore, gulls are not pure soaring birds but need a certain amount of muscle power. So, in order to achieve the higher performance requirement, the larger species must have a relatively stronger muscle structure for flying. This, however, cannot be inferred from Dinnendahl and Kramer's breastbone measurements, and my studies led to the same results (Table 6). Should this prove to be true, the rate of descent of the smaller species cannot be assumed to be any less than that of the large gulls. If we assume it to be more or less the same for all four species, and for this purpose it is irrelevant whether or not the figures indicated by Schmitz for the silvery gulls are correct, we have a solid basis for calculating the gliding speed and evaluating the glide ratio. According to the formulas of Table 2, $v_y = v_x \epsilon$. When the gliding angle is flat, the horizontal speed v_x is equal to the gliding speed v . The formula is accordingly:

$$v = \frac{v_y}{\epsilon}$$

Based on Kramer's table we can assume either the glide ratios or gliding speeds to be correct and then calculate the other respective values with the help of the known rate of descent as I have done in Table 5 (lines 2 and 3 for each species). Both methods result in the necessary agreement of the performance requirement with muscle

¹ Cf. Schmitz, op. cit., pp. 17 and 19. The misinterpretation of the glide ration is the basis for Dinnendahl and Kramer's false conclusions.

performance.¹

This result can be stated more precisely: if different gull species have the same flying capabilities, either the gliding speed /463 of the smaller species must be higher, as maintained by Dinnendahl and Kramer, or their glide ratio must have undergone further decrease.

The only way to determine this is through measurements of speed. I performed a number of such measurements but unfortunately, the results were less than perfect. The difficulties lie in the fact that wind usually cannot be adequately evaluated from the place of the observer owing to the distance of the gulls and the fact that the birds often soar with reduced speed near beaches. Based on the figures available thus far, which are for the most part lower, I would venture to say that the gliding speeds given by Dinnendahl and Kramer are only approximations of the truth and that resultant glide ratios are therefore incorrect. Schmitz' conclusion that the glide ratio increases by a factor of 2 when size is increased by a factor of 10 is probably not applicable to small changes in size since the glide ratio does not follow a straight line function, as was assumed by Dinnendahl and Kramer in their calculations. It may well be that the glide ratio decreases faster with increasing Reynolds numbers than when the figures are higher. This supposition is based on the fact that birds are absolute flying bodies with a low range above the critical minimum for flight.

The following fact is involved: in the case of small flying bodies, a laminar or fully turbulent-free stream flows at a low speed (low Re number) behind the profile nose reducing the suction on the upper portion of the wing to a fraction (Figure 3). Lift is then less than resistance and the aircraft pitches down. At another critical

¹ The precision of the agreement between the relative figures should not cause surprise. It is based on allometric calculations where muscle performance and weight were taken as parallel elements.

Re number, which is different for each profile, the stream will suddenly pick up again and cause a dramatic decrease in resistance and an increase in lift thus restoring flight capability. This occurs according to the border layer theory of Prandtl (1935) because a very thin border layer becomes turbulent on the upper side of the wing and transmits energy to the wing through the build-up of a vortex. The critical numbers lie for the most part between 150,000 and 20,000 depending on the profile. Consequently, large aircraft, which fly at high Re numbers (the number for Schmitz' small glider was already up to 1.5 million; others were as high as several million according to size and speed) are always above the critical flight threshold. However, /464 models always fly close to the critical Re number and they often fly below the critical threshold and stall. Rising above the critical level is then achieved through the artificial production of turbulence. Birds fall within the range of aircraft models and their Re numbers. In Table 7 I have compiled Re numbers for a variety of species in so far as I was able to calculate the average wing chords and obtain data on speeds. The critical Re numbers of the species concerned were impossible to determine in the absence of a wind tunnel, but it is certain that the range above the critical threshold, i.e., the difference between the critical number and the Re number at which the bird actually flies, is relatively small. Figure 3 shows that the curve of the glide ratio is steeper in the range of unstable Re numbers than in the range of higher Re numbers. The illustration is based on /465

Table 6

Length of the crista sterni as a percentage of the AS length in gulls

25 <i>Larus ridibundus</i>	30.2
52 <i>Larus canus</i>	30.0
75 <i>Larus argentatus</i>	28.1
19 <i>Larus marinus</i>	28.4

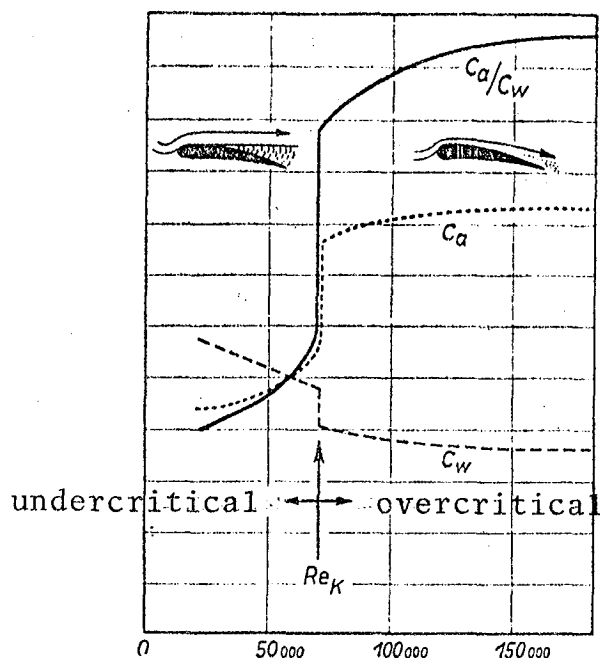


Figure 3. Transition from undercritical (laminar) to overcritical (turbulent) airstream on a wing profile with increasing Re number.

$Re_K = 63,000$. The lift coefficient c_a increases suddenly, the resistance coefficient decreases suddenly. For reasons of facility, the reciprocal $\frac{c_a}{c_w}$ of the glide ratio $\frac{c_w}{c_a}$ appears

and increases dramatically (the scales are different for the coefficients and reciprocal glide ratios). Simplified from Schmitz.

the ratios of one and the same aircraft model, and any change in the Reynolds number can take place only through an increase in speed, whereas it appears to be the result of size increase in our comparisons. Although I possess no proof to this effect, we can presume that the glide ratio function is similar in this case.

This theory is in my opinion the only one capable of reconciling the antinomy mentioned above.

Table 7
Calculation of Reynolds Numbers

Species	Average wing chord t mm	Speed v msec	Re = t·v·70
Larus ridibundus	110	7.7	59,000
Larus canus	130	7.8	71,000
Larus argentatus	157	10	110,000
Larus marinus	170	10.5	125,000
Coloeus monedula	127	12	107,000
Corvus corone	184	12	155,000
Corvus corax	205	14	200,000
Anas crecca	74	>33	>171,000
Anas boschas	116	<29	<235,000
Anser anser	180	19.5	246,000

III. Allometry and Transposition

Our study thus far raises a new question. When the overproportional increase in wing loading is adaptive within the size range of gulls but not beyond that range, how do body size and wing surfaces react in the case of birds comparable to but larger than gulls? Albatrosses are the only birds for which this question is relevant. I have had to take published data for their measurements. I found useful documentation for Diomedea irrorata and exulans in Schmitz' research and also in his data on an "albatross," which are very close to those of the Diomedea exulans and perhaps actually taken from that species. Table 8 shows that these albatrosses have, as expected, higher wing loadings than gulls, but the true relationship between the two groups is shown in the diagram of Figure 4. Like gulls, albatrosses have negative wing allometries, but the significance of the two cases is different. The allometric line of the albatross' wing surfaces is not a continuation of the gull but actually opposes it on a graph as compensation for negative allometry. This is repeated on

a new level.

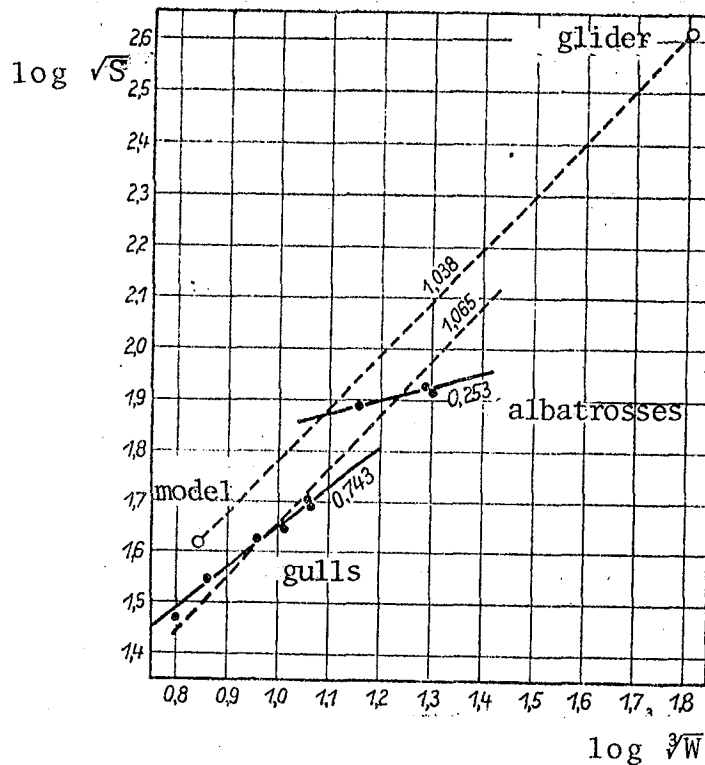


Figure 4. Allometric relations for gulls and albatrosses (soaring birds), and aircraft model and glider. Negative allometry within both bird groups, transposition with positive exponents. The allometric relation between aircraft model and glider is parallel to this transposition. Double logarithmic graph.

The wing loadings were accordingly placed against one another in opposite directions as dictated by the reciprocal character of the loading. The albatross line was thus lowered. I used to call these different levels of wing loading loading levels (1951). The large albatrosses have a higher loading than the large gulls (and the small albatrosses a higher loading than the small species of gulls), but a lower loading level or wing loading than gulls of a comparable size.

The extension of the curves towards one another is defined by the factor b of the allometric equation or, in the case of wing loading, $\frac{1}{b}$.

The fact that there exists no soaring bird with greater loading than the large albatross confirms the theory that a further size increase in gulls is not possible given their negative allometry. At the size of a large albatross such a bird would have a wing loading of 15 kg/m^2 as compared with 10 kg/m^2 for the true albatross. (Schmitz' figure, op. cit., p. 18, of 16 kg/m^2 is a printing error.) The adaptation value of negative wing allometry does not begin to disappear only after a size increase has attained gigantic proportions, as stated earlier, but does so even with a fairly modest size increase.

The empirically discovered curve extension is also a logical imperative. It is only in this way that we can even conceive of a size increase above and beyond the limits determined by negative allometry.

I suggest the closely related term transposition (Herre, 1956) to describe this kind of extension of allometric curves towards one another. The scale of transposition can be determined using the allometric equation once the midpoints¹ of each allometric curve have been joined.

The transposition line obtained in this way and shown in Figure 4 has the exponent $a = 1.056$. I should like to counter the arguments that so small a deviation from isometry ($a = 1.00$) cannot be evaluated and can thus be considered isometric for all practical purposes for the relationship between the model and glider. The radical aerodynamic change discussed earlier of a wing loading increase by a factor of 8 rather than 10 is expressed in the allometric equation by the exponent $a = 1.038$, an even smaller deviation from isometry. The aircraft's allometry is illustrated in Figure 5. It is doubtless of interest that the wing surface allometry from the model to the glider is a straight line in a double logarithmic graph, and that this straight

¹ If the original allometric curves are based on the size variation of the adult individuals of a species using a sufficient number of individuals, correct midpoints are found. In the case of interspecific allometries the distribution of individual values (of the species) depends on conditions having nothing to do with variation.

runs parallel to the transposition line running between gulls and albatrosses.

Allometric consideration of the relations between different groups is by no means new, but conceptual limitation is. Numerous allometries dealt with in the literature are in reality transpositions, i.e., they /468 establish the means of transposition of individual allometries, and it is not always as easy to recognize the underlying law as it is in the case of the functional necessities of flight. The wide-spread use of the allometric formula in transpositions, for which examples are not necessary, does, however, prove its practical usefulness in computing such transpositions.

Transpositions of wing allometry can be determined for the mere comparison of small and large birds as long as bird groups are chosen whose wing shape and flight are comparable enough to consider them as examples of the same basic plan on different size levels. I compiled the material in Table 8 to this effect. In order to extend the number of species I took data on several additional species from Savile (op. cit., p. 215) where such species belonged to the groups I had studied.

Since this very important piece of research will doubtless be used to evaluate morphological and aerodynamic problems, it is necessary to point out a few obvious errors in Savile's tables of measurement, which could easily lead to misinterpretation.

He indicates a wing spread of 81.8 cm for the American peregrine falcon weighing 1222 g. This wing spread is not possible. The weight is obviously that of a female, which must have a wing spread of 110 cm by analogy with the German peregrine falcon.² Even the minimal wing-

The midpoints of such curves can therefore be understood only as lying midway between the largest and smallest species.

² Translator's note: As stated earlier, there seems to be a confusion in Dr. Meunier's use of the biological symbols for male and female, unless the species mentioned here have females larger than the males.

spread of the male cannot be less than 90 cm (97.8 cm according to Fisher, 1893). In the case of the red-tailed hawk (Buteo jamaicensis borcalis) the weight of 1267 g is that of a female, and the wing spread of 110.5 cm lies under that of the male (according to Fisher, a minimum of 124.5 cm).

I took Savile's classification of birds according to their wing shapes as a basis but was unable to respect all details. Following his example I grouped small birds and crows together as representative of the ellipsoid winged birds. The qualifying remark must be made here that the group of small birds is relatively heterogeneous since it includes round-winged birds (Accentor modularis) and narrow-winged birds (Eremophila alpestris) whose wing forms have ecological significance: (forest or open countryside), as Savile himself emphasized. In order to preclude arbitrary choices I included all species for which I had material myself or could find in Savile's work. I find it remarkable that despite the doubts expressed, the results should be such a clearly negative allometry as shown in Figure 5.

Under the heading of birds with a high aspect ratio, Savile compiled such heterogeneous birds as Diomedea, Larus, Cygnus, Gavia. I find this impossible because of the different manners of flight and /469 wing loading. I have therefore separated the albatrosses and gulls or soaring birds (Figure 4) from the swans and other anatidae or non-soarers (Figure 6). This is an important distinction since swans and /472 small anatidae never soar. Both Savile and the literature in general place ducks in the high-speed category. I consider it significant, however, that swan wings are the same type but increased in size and that all particularities, such as the frequency of wing stroke, result from size. Ducks are also distinguished among the other high-speed birds (falcons, wading birds, soaring birds) in that they do not possess the striking wing sweepback, the aerodynamic significance of which is still unexplained (Savile, op. cit.).

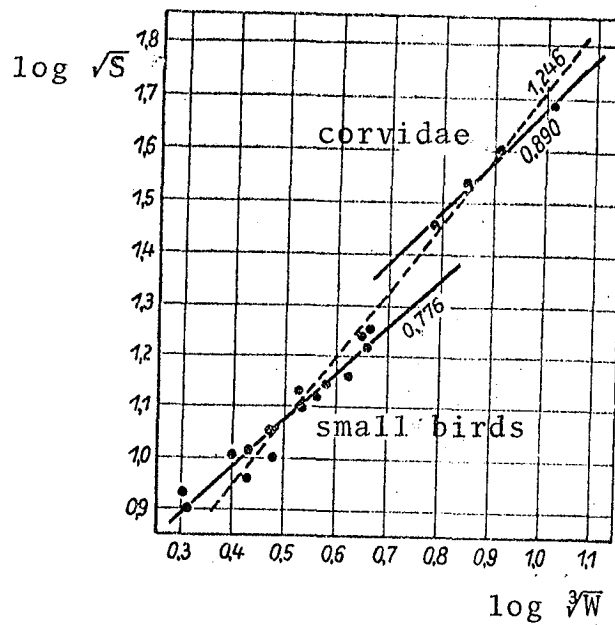


Figure 5. Negative allometry and positive transposition in small passeridae and corvidae (ellipsoid wings). Double logarithmic graph.

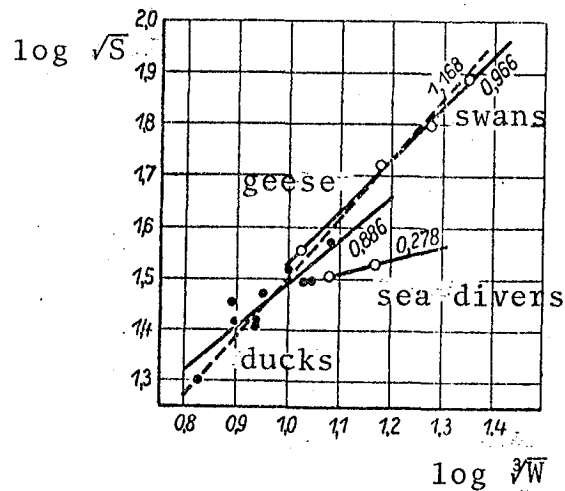


Figure 6. Allometry of bird species with flapping wings (anserae). Taking ducks as one group and geese and swans as another, negative allometry and positive transposition result for both. Very negative allometry for the sea diver (Gaviidae). Double logarithmic graph.

Table 8

Aerodynamic measurements of bird species grouped according to wing shape and flight

Organization within each group according to size

Taken from Savile 1957

Species and type	Weight W g	Wing surface S cm ²	Wing loading W S kg/m ²	Wing span d cm	Wing spread $\Lambda = \frac{d^2}{S}$
Ellipsoid-winged birds					
Small passeridae					
* <i>Certhia familiaris americana</i>	8.3	74	1.12	18.3	4.65
* <i>Dendroica petechia</i>	8.8	64	1.37	17.5	4.78
<i>Anthus pratensis</i>	16.0	102	1.57		
<i>Accentor modularis</i>	19.6	82	2.39	20.0	4.88
<i>Fringilla montifrigilla</i>	20.0	107	1.87		
<i>Fringilla coelebs</i>	26.2	132	1.98	27.3	5.66
<i>Passer domesticus</i>	27.6	100	2.76	23.1	5.34
* <i>Eremophila alpestris</i>	38.6	183	2.10	32.5	5.79
* <i>Dumetella carolinensis</i>	40.5	157	2.58	27.2	4.70
* <i>Molothrus ater</i>	48.9	173	2.83	31.0	5.57
<i>Turdus musicus</i>	52.0	193	2.69		
<i>Sturnus vulgaris</i>	75.0	210	3.57	38.2	6.96
<i>Turdus pilaris</i>	90.7	305	2.97	44.3	6.45
<i>Turdus torquatus</i>	95.2	274	3.47		
<i>Turdus merula</i>	99.3	325	3.05	40.3	5.90
Corvidae					
<i>Colocus monedula</i>	232	814	2.85	69.2	5.89
* <i>Corvus brachyrhynchos</i>	361	1190	3.03	85.2	6.16
<i>Corvus corone</i>	568	1525	3.72	98.0	6.30
<i>Corvus corax</i>	1175	2370	4.96	135.0	8.77
Accipitridae					
High lift					
<i>Buteo buteo</i> ♂	792	2129	3.72	119.0	6.67
<i>Buteo buteo</i> ♀	1030	2305	4.46	126.0	6.88
* <i>Aquila chrysaetos</i>	4415	5030	8.78	194.0	7.48
Maneuverability					
<i>Accipiter nisus</i> ♂	144	633	2.28	62.5	6.18
<i>Accipiter nisus</i> ♀	266	832	3.20	72.0	6.24
<i>Accipiter gentilis</i> ♂	720	1521	4.73	98.5	6.39
<i>Accipiter gentilis</i> ♀	1145	1835	6.54	110.0	6.54

Table 8, Part 2

Species and type	Weight W G	Wing sur- face S cm ²	Wing loading W S kg/m ²	Wing span d cm	Wing spread $\Lambda = \frac{d^2}{S}$
Laridae and Diomedudae					
Gulls					
<i>Larus ridibundus</i>	251	872	2.88	94.0	10.15
<i>Larus canus</i>	388	1249	3.11	113.0	10.21
<i>Larus fuscus</i>	764	1789	4.26		
<i>Larus argentatus</i>	1111	1946	5.71	143.0	10.50
<i>Larus marinus ad.</i>	1509	2543	5.93	164.0	10.58
<i>Larus marinus juv.</i>	1549	2380	6.50	158.0	10.50
Albatrosses					
* <i>Diomedea irrorata</i>	2040	5960	3.42	231.3	15.00
* <i>Diomedea exulans</i>	8160	6800	12.00	345.5	17.25
„Albatross“	7500	7200	10.41	380.0	20.00
Anatidae					
Ducks					
<i>Anas crecca</i>	300	399	7.52	54	7.32
<i>Aix galericulata</i>	475	814	5.84		
<i>Poecilonetta bahamiensis</i>	495	680	7.25		
<i>Anas penelope</i>	650	658	9.91		
* <i>Spatula clypeata</i>	652	669	9.75	73.5	8.10
<i>Anas strepera</i>	720	883	8.16		
<i>Anas boschas</i>	1010	1079	9.35	84	7.78
* <i>Anas rubripes</i>	1245	980	12.70	82.5	7.00
<i>Melanitta fusca</i>	1370	983	13.92		
<i>Somateria mollissima</i>	1770	1404	12.60	104	7.68
Geese and swans					
<i>Branta bernicla hrota</i>	1190	1299	9.18	106	8.66
<i>Anser anser</i>	3458	2796	12.37	149	7.95
* <i>Cygnus columbianus</i>	6800	3980	17.08	184	8.52
<i>Cygnus olor</i>	11300	6033	18.72	223	8.25
Gavidae					
<i>Gavia stellata</i>	1760	1010	17.4		
* <i>Gavia immer</i>	3260	1336	24.4	117	10.0

Aspect ratio A is a measurement for the length of a wing in relation to its surface and increases in value as the relative width of the wing decreases. A high aspect ratio is aerodynamically advantageous because it improves the airstream ratio. The table shows that A increases with body size in the individual groups. It is thus clear that the wing undergoes shape changes that increase lift when body size increases. However, this is particularly elusive among the anserae. Swans do not have a particularly high aspect ratio in comparison with ducks and geese, but the entire group does possess a stretched wing relative to the non-soaring ellipsoid-winged birds. It can be regarded as homogeneous as to wing shape.

Among the accipitridae (Figure 7) the hawk and sparrow hawk possess the identical wing type: short, broad wings, long tails, high maneuverability, and high initial speed. All of these qualities are suited to hunting in shrub and forest land. Furthermore, the sex difference in the sizes of both species is so great that the sexes can be considered aerodynamically as different sized species of the same type. There are thus four levels within one type. A similar situation exists between the common buzzard and the golden eagle (soaring birds).

A comparison of the allometric diagrams (Figures 4 to 7) show that the same principles are applicable to each one. The allometric curves of the individual size levels are placed in such a way as to compensate for the allometry of the others. The placement of the curve is particularly impressive in the sparrow hawk-hawk group because the similarity in body build is more apparent than in others. Contrary to other groups, the buzzard-eagle group shows negative transposition. This means that a size increase decreases the negative allometric tendency but does not cause positive transposition at this size level. I am convinced that this would take place with a further size increase. The data from Bonelli's eagle (Hierasetus fasciatus) and the harpy eagle (Harpia harpyia) are of interest. The range of species of anatidae from duck to geese and swans can be presented in

such a way that all species are compiled into a single curve, which would be allometrically positive on the average, but this cannot be conclusively proven based on available material. In fact, obtaining statistical proof for interspecific diagrams is a general problem. The a values are introduced as regression coefficients¹ in double logarithmic graphs. This is the only possibility available owing to the low number of individual values. The individual values or specific figures cannot be increased, and the number of individuals, which is considerable in the case of some species, cannot be used for statistical proof of interspecific allometry because it is different for /474 each species.

In examining this diagram we must be aware of the fact that they are not simple systems consisting of no more than allometric curves

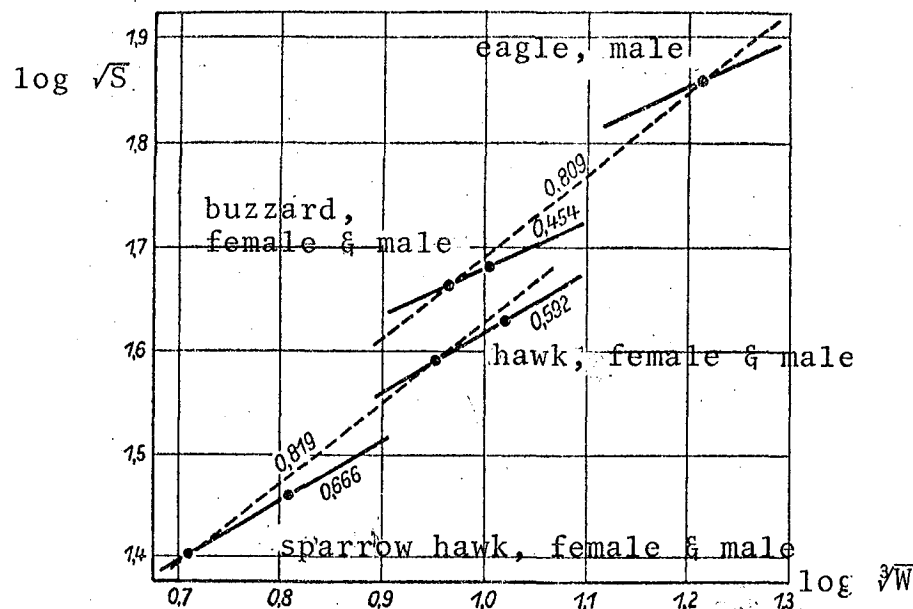


Figure 7. Transposition between two raptorial bird types with four size levels for each.

1. sparrow hawk-hawk type (Accipiter): high wing loading, powerful muscles, maneuverability, transposition to a new level
2. buzzard-eagle type (Buteo-Aquila): lower wing loading, weaker flight muscles, high lift. The eagle is transposed against the buzzard (which can be recognized although the intraspecific allometry of the eagle can be drawn only by analogy with the buzzard). There is no true transposition between hawk and buzzard because they are

Figure 7, continued: of different types and sizes. Double logarithmic graph.

on the one hand and relative transposition curves on the other hand. In actuality there exists an entire hierarchy of relationships. The interspecific curves referred to here as allometric are undoubtedly transpositions of intraspecific allometries not identified with them, and these may in turn be transpositions of the allometric curves of individual sexes, as I have actually established (although this conclusion is as yet unpublished).

Similar relations may exist among many known allometries. Lack of material and the studies done on heterogeneous animals using the allometric equation without examining their inner allometries have prevented these relations from becoming widely known. In general, all allometric relationships must be seen as a part of a transposition system.

IV. Evolutionary Significance

We do not need to limit ourselves to the effect of size increase on models series. Examples of experimental size increase of different bird species exist for domestic birds. Table 9 is a compilation of body size, wing loading, and flight capability of domestic ducks, geese, and chickens in comparison with their wild counterparts, the mallards, gray geese, and black grouse (I was unable to obtain jungle fowl, but its measurements must resemble those available for bantam chickens).

As the table indicates, only those poultry species having essentially retained their initial size (high flying ducks and bantams) maintained their flight capability. In comparison with their prototypes, species which have increased considerably in size have lost

¹ cf. Frick, 1957.

their flight capability (German farmyard duck, blue sparrow hawk) or greatly reduced it (Diepholz goose). The loss of flight power is undoubtedly caused by the overproportional wing loading or negative wing allometry which preceded. I do not possess sufficient material to calculate the specific allometric curves of the mallard duck and gray goose. (In the case of the mallard duck there would seem to be two separate curves for the two sexes.) I am therefore unable to prove whether or not the allometry between the prototype and the larger domestic species (cf. table) actually concurs with the intraspecific allometry of the wild species, but the important fact in aerodynamic /475

Table 9

Wing loading and flight capability of different sized domestic birds,
in comparison with their wild counterparts

Species	W	S	G S	Flight capability	Allometric ex- ponent a of the wing from wild to domes- ticated species
Mallard duck, female	940	807	11.6	total	
High flying duck, female	1050	823	12.8	total	
Farmyard duck, female	1570	971	16.2	none	0.533
Gray goose, femals	3050	2195	13.9	total	
Domestic goose, female	5720	2932	19.5	limited	0.374
Black grouse, male	1250	950	13.2	total	
Bantam chicken, female	527	600	8.8	good	
Shabo, female	575	838	7.0	very good	
Dutch white crested, female	740	862	8.6	limited	
Blue sparrow hawk, female	2350	1140	20.6	none	

evaluation is that a pre-existing negative allometric relation brought about inability to fly at the time of very small size increases. If Dinnendahl and Kramer are correct about the usefulness of this to all sizes, large species would have to fly as well as small and wild species. However, every chickenyard proves that the opposite is true,

and this observation should have the effect of keeping these authors from their conclusions.

It could be objected here that it is perhaps not the increase in wing loading that prevents flight but the influence of domestication instead. This argument is unsound, however, since pure domestication influences had to have had their effect on all sizes. The ratios among domestic chickens are somewhat more confusing. They have obviously experienced mutations in the length of primaries even among species of the same size. An example of this are the bantam chicken species I studied in which one (shabo) had a much larger wing surface (838 cm^2) for the same body size than the others (600 cm^2). The shabo's flight is correspondingly superior.¹

It can be assumed that the muscles of non-flying species are less developed, and the question can be posed whether or not this was /476 the actual cause of the loss of flight capability. Prof. Herre provided me with muscle weights of gray and domestic geese. These data show that the m. pectoralis major was on the average 17.7% of the total weight for six gray geese and only 11.7% for 8 domestic geese. I consider this not to be a cause but a secondary factor instead. I myself compared the size of the sternum of the gray goose and domestic goose as the product of the length from the crista to the tip, the upper width of the sternum, and the height of the crista. This product, which is to a certain extent analogous with the possible muscle mass, was 10.8% of the total weight for the gray goose and 9.0% for the domestic goose. The difference is considerably smaller than with the muscles and should be considered as a result of nonuse.

Although we can assume that the intraspecific allometry of wild species was perpetrated in the domestication of new size magnitudes, we cannot assume this to have taken place as a normal evolutionary

¹ Flight capability can also be limited through mutations of this kind. There does not appear to be any species that increased greatly in

allometric progression or continuation of ontogenetic growth. We saw that this is mere order allometry concerning the product of an inherited function plan. This fixed function plan must comprise hypothetical sizes, which would involve excessive form distortion were they to be attained and render the vital function of flight impossible.¹ However, domestication is not a true phylogenetic development as Herre continually points out (Herre, 1959). His theory that the process of domestication throws light on prototype development proves here to be a fruitful one. True evolution is obviously dependent on mutations enabling a size increase while retaining the earlier functional capabilities. When a small bird acquires crow size or the sparrow hawk, hawk size without mutation, greater specialization can result and in some cases extinction. Dinnendahl and Kramer have attributed the opinion that negative wing allometry cannot be changed through evolution to me. I was unaware that I had ever stated this. I had referred /477 to the species Larus fuscus and argentatus in which allometry fails to run in conjunction with body size even for one group of the same origin. I specifically indicated that non-allometric changes in the wing proportions of the birds had to be unusually frequent (op. cit., p. 429). I did not misinterpret the allometry of the gull wing. This does not mean, however, that a size increase on the basis of existing wing allometry cannot take place in certain cases as it did with domestic birds. I do not regard this as a true evolutionary process but rather as evolutionary failure leading to limited specialization with, in some cases, the danger of extinction. The best example of this is still the brain of the huge saurians. If mamals had increased in size according to the measurement of their intraspecific brain allometry, a similar error would have taken place (Roehrs, 1958). This was avoided in mamals since transpositions clearly occur all the time, but it was not in the case of the saurians.

size with full retention of flight capability. Of course, only similar types can be compared that have not undergone further and dissimilar mutations. In this case, the reduction in flight capability with size increase is an absolute law.

¹ As long as mutational transposition does not counteract the effects of allometry and shift it to a different level.

In the case of simultaneously phylogenetic and mutational size increase in a bird, not only is the transition to a new wing allometry through mutational transition necessary but also an overall build comprising many details. This can be seen on the wing itself in the increase in the aspect ratio (Figure 8), which increases lift power. The increased curvature of the wing, for example, has a similar effect on large eagles as compared with smaller raptorial birds as does the increase in the slotting of the wing, an area in which Savile did a great amount of research (op. cit.). This wing slotting takes place through a narrowing of the distal parts of the primaries. This serves to create turbulence in the border layer of the air stream. This indicates that although negative wing allometry discourages lift, it is part of a complicated whole and probably intended not only to increase loading but also to achieve better wing manipulation. The comparison of jackdaws and common crows, which was so highly recommended to me by Dinnendahl and Kramer, shows not only a continuation in the allometric curve but also a vastly complicated process of reconstruction, which is shown in Figure 8. It is clear here that a greater aspect ratio and more defined slotting increase lift.

Savile's work on wing construction and flight capabilities of the loon (Gavia) is of great interest. He demonstrates by means of the surface law and without touching on allometric problems that a /478 phylogenetic size increase of this bird did not bring about the necessary relative wing increase and improvement of wing construction. He writes as follows about the Gavia immer: "Under these handicaps the common Loon takes off only with difficulty, after a long run and clings shallowly... The smaller red-throated Loon (G. stellata) and Pacific Loon (G. artica pacifica) evidently have substantially lower wing loadings, for they take off with less labor." He goes on to say (op. cit., p. 223): "As the body weight increased, the genetically rigid wing failed to develop in compensation," It is obvious to me that he is referring here to what occurred in domestic birds.

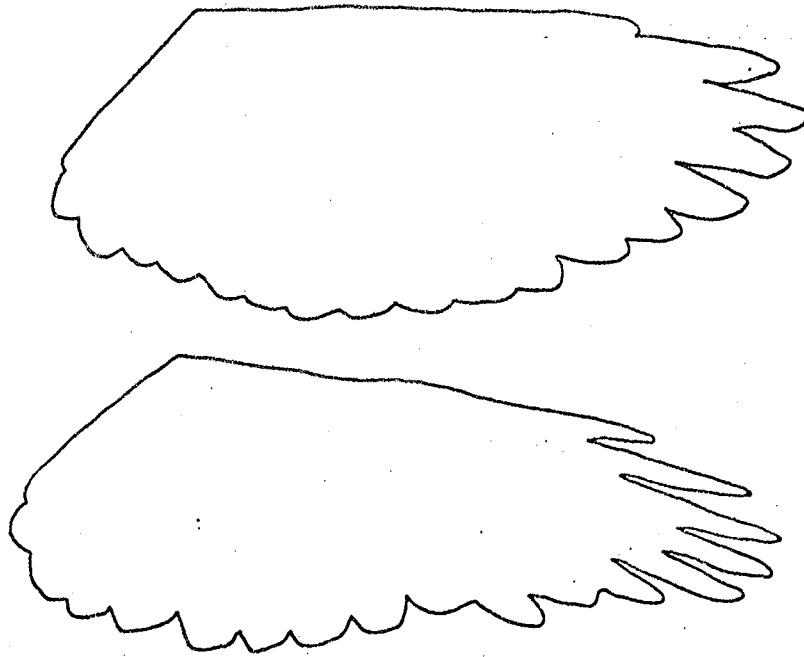


Figure 8. Wing sketch of a jackdaw(Colocys monedula) above and common crow (Corvus corax) below, modified to the same size. The length of the wings from the front edge angle to the tip is 53.5 cm for the common crow and 30 cm for the jackdaw. The common crow indicates aerodynamic shape improvements: increased wing spread and slotting.

I have added data on the wing loading of the Gavia stellata to Savile's data on the Gavia immer and compiled them in Figure 6. The somatic exponent between the two species is remarkagly low. Even if it increases when more material is obtained, the higher loading of negative allometry must lead more quickly to a loss of flight capability than with birds having lower wing loadings. The great northern diver uses its wings not only during migration but also according to /479 Savile for daily feeding, since it often breeds on small lakes with insufficient food supplies. It has attained a size which cannot be surpassed without fundamental construction changes and obviously suffers a disadvantage in comparison with smaller species, since no aerodynamic improvements in its wing form have taken place. This is all the more interesting since the common loon does not use its wings for paddling under water and thus has not damaged its means of flight

in a developmental adaptation to this task. I indicated earlier that when the great auk actually did lose its flight capability, a similar development may have taken place with the difference that the biotope made the ecological limitation of flight loss possible for this bird.

To express this idea more explicitly, the results of evolutionary size increase are fundamentally dependent on the surface law. Allometry can be an adaptive aid in the case of small size increases but also increases the rigidity of size limitation. Since, however, I do not consider such stagnation as being a normal evolutionary process but rather as an exception, the contradiction between Dinnendahl and Kramer and myself concerning the problem of allometry is smaller than it appears.

Conclusion

The allometry of primaries as a function of body size is positive in growing birds but negative in adult birds. This inversion occurs because large birds do not pass through the same growth stages as small ones. Individual growth curves are determined very early according to the adult size towards which they are headed. It is therefore necessary to make a fundamental distinction between growth allometry and order allometry.

Negative wing allometry increases wing loading as a bird's size increases because of the surface law. This probably has an adaptive effect within a limited size span owing to the aerodynamic improvement through the Reynolds number. Once beyond this size range, wing loading must be decreased through a major proportion shift, as is the case in many bird groups. Negative allometry is thus retained on a higher level. Should this shift in proportions or transposition fail to take place as is the case with domestic birds, the result is a loss of flight power.

/480

Evolutionary increases in size are normally accompanied by transposition. Flightless birds may result when transpositions fail to take place. Continued allometry beyond the former size range is not a further perpetration of ontogenetic growth but of an inherited proportion plan.

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Remarks Concerning the Revision

/481

In an oral discussion on the aerodynamic aspects of these problems, to which I was kindly invited by Dr. Kramer and Dr. Focke, honorary professor of engineering, on January 12, 1959 in Bremen, Dr. Focke explicitly confirmed that the basic standard of soaring capability (ascent capability in updrafts) is the rate of descent and not the glide angle. I had originally expressed this idea, based on Schmitz' work, in a discussion with Dr. Kramer at a meeting of the German Ornithological Association in Kiel on September 1958 (cf. pp. 455,461). A larger bird is thus at a disadvantage compared with a smaller one despite its improved glide ratio if it has a greater rate of descent.

The possibility thus ensues that the figures indicated by Dinnendahl and Kramer (op. cit.) in their Table 1 (which I repeated in the first line of each species in my Table 5) imply aerodynamic improvement with increased size, as was the authors' assumption. This was the basis of their criticism of my theory and assumption that a size limitation must exist owing to increased wing loading.

Although I did regard negative wing allometry both within a species and somewhat beyond as being probably adaptive, which agrees with Dinnendahl and Kramer, this does not mean that the goal of such adaptation is higher wing loading. It is quite possible that an adaptation to other requirements is more important. Dr. Focke has stated in this regard that in aircraft construction the wing weight plays a role since it increases by an exponent of 3, as compared with the wing surface, which increases by an exponent of 2 (Lanchester's law). It seems improbable to me the wing weight should cause negative allometry since this concerns only feathers (p. 444), which, from the standpoint of weight, could not play the role played by comparable parts of thick airplane wings. It is also difficult to reconcile transposition with the necessity of negative allometry based on wing weight or stability since both must proceed along an allometric curve without shifts. Until we are able to obtain better aerodynamic data on individual species (gulls) for glide angles, gliding speeds, and rates of descent, the most probable hypothesis in my opinion is that within a limited area the necessity for overproportional wing loading causes negative allometry. This hypothesis does not question the theory /482 advocated by myself and others (p. 453) that there exists a size limitation owing to increased wing loading, without prejudice to the arguments against such size limitation based on stability and performance difficulties.

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